

Notes on Grapsoid Crabs from the Raffles Museum, Nos. 3, 4 and 5¹

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3. Faunal Differentiation in the regions east and west of the Malay Peninsula

In the course of my studies of the mangrove and littoral Grapsoids of Malaya and Borneo I have been struck by unmistakeable signs of specific and subspecific differentiation between the fauna of Malaya's west coast and those of its east coast and north-western Borneo.

A few species have been collected in all of these localities and a much larger number in one or more of them. I do not propose to list all of these as in many cases such incidence is due to environmental conditions or, in the case of rare species, to their having been missed by collectors.

The following lists are of species which my experience in collecting these crabs leads me to believe have a restricted distribution within the region we are considering.

West Coast of Malaya: *Dotilopsis brevitaris* (de Man); *Ilyoplax longicarpa* Tweedie; *Scopimera proxima* Kemp; *Uca rosea* (Tweedie); *Metaplex crenulatus* (Gerst.); *Sesarma onychophora* de Man. Of these only *U. rosea* has been taken at Singapore.

East coast of Malaya: *Camptandrium elongatum* Rathbun. Also taken at Singapore.

North-west Borneo: *Dotilloplax kemp*i Tweedie; *Ilyoplax spinimera* Tweedie; *Uca angustifrons* (de Man); *Uca rhizophorae* Tweedie; *Metaplex tredecim* Tweedie; *Sesarma lepida* Tweedie; *S. rectipectinata* Tweedie; *S. semperi* Burger; *S. johorensis* Tweedie. Of these the last two occur also at Singapore, *S. johorensis* having been described from the shore of the Johore Strait opposite Singapore Island.

Scopimera intermedia Balss has been taken in Borneo, eastern Malaya and Singapore. The west coast species listed, which are not actually restricted to that region, have a distribution to the west of Malaysia and the rest to the east of Malaysia.

¹. Continued from Bull. Raffles Museum, 23, 1950: 310-324.

Although the lists throw most emphasis on distinct Malayan and Bornean mangrove-haunting Grapsoid faunas there is some indication that eastern Malaya has a closer affinity with north-west Borneo than with the west coast of the Peninsula; the forms found at Singapore are more usually those of the eastern than the western region. This affinity is more clearly indicated, however, by subspeciation in certain species which are found in both the western and eastern regions.

Ilyoplax delsmanni (de Man) was described from the Bay of Batavia. Specimens are in the Raffles Museum collection from Muar, Port Swettenham and Prai, localities on the west coast of Malaya, from Singapore Island and from the Karimon Islands, south-west of Singapore. The subspecies *serrata* Shen (*yuhana* Rathbun) was described from Amoy and Fukien, and has been collected at Mersing and Kuala Sedili on the east coast of Johore, and in the Kuching River, Sarawak.

Here a China Sea and a western Malaysian form are evidently distinct, the latter occurring in western Java, on the west coast of Malaya and at Singapore.

Sesarma kraussi de Man was described from Mergui and has been collected at Port Swettenham and Prai. The subspecies *borneensis* Tweedie was described from Labuan (Borneo) and in Malaya has been found only at Singapore. Here the eastern race is found at Singapore.

The crabs described above are all littoral forms found mainly in mangrove swamp. The land crab, *Gecarcoidea humei*, shows what appears to be subspecific differentiation in the western and eastern Malaysian areas, but as it is normally an inhabitant of small islands, different localities from those frequented by the Grapsids and Ocypodids have to be considered.

In separating the Christmas Island form, *G. h. natalis* from material from the Andaman Islands I used as a character the numerical expression derived from counting the total number of spines in the superior single row of spines on all eight ambulatory dactyli. The average figure for *natalis* was determined as 33; in two specimens from the Andamans it was 75 and 81. The figure illustrating Wood-Mason's original description is of a male, and is drawn in considerable detail; the count in this specimen appears to be about 77.

On an expedition to some of the islands in the Malacca Strait in January 1953 some specimens of *G. humei* were collected, and spine counts were as follows:—

Jarak Island (males): 92, 93, 94, 97.

Rumbia Island (males): 84, 85, 88, 98, 99; (female): 112.

Berhala Island (male): 82.

The coloration of the Malacca Strait specimens agrees well with that described by Wood-Mason for the typical form from the Nicobar Islands, and I incline at present to regard as typical populations in which the figure averages above 70 and below 100 in males. This would place the Andaman, Nicobar and Malacca Strait populations in *G. h. humei*, with a possibility that large series might establish the validity of a rather higher count in Malacca Strait Specimens.

A series of three specimens collected at Aor Island in the South China Sea in 1938, and recorded in 1949, have the counts 115 (male), 121, 155 (females). The specimen reported previously as damaged has a leg severed, but it is still present in the storage bottle. I can find no other characters to separate the Aor, or South China Sea form, and do not propose to give it taxonomic recognition on so short a series. Nevertheless I believe that here again is an indication of a differentiation of eastern and western Malaysian littoral or marine-amphibious faunas.

On p. 86 of Professor de Beaufort's book *Zoogeography of the Land and Inland Waters* is a series of maps of Sundaland during various stages in the Pleistocene. According to them two marine gulfs existed during the periods of interglacial ingression of the sea, one situated in the region of the north part of the Malacca Strait, the other occupying most of the area of southern Sumatra. Both are connected with the Indian Ocean, but not, as the Malacca Strait is now, with the South China Sea. The map illustrating the condition during the second interglacial is reproduced, by kind permission of the author and publishers at fig. 1.

If these reconstructions are accepted it becomes clear that the littoral waters of the area now represented by the Bay of Bengal and the Malacca Strait were cut off by the whole of the great peninsula of Sundaland from those of the South China Sea throughout the Pleistocene, even during the interglacial marine ingressions. The post-glacial marine ingression has resulted in a marine connection south of the Malay Peninsula, but the faunal differentiation resulting from the long period of separation of the two areas by intervening land has persisted, with a meeting and some degree of mixing in the region of Singapore.

The existence of distinct subspecies of Sea Snakes on Malaya's east and west coasts may be supposed to have originated in the same way. *Hydrophis torquatus torquatus* Günther and *H. fasciatus fasciatus* (Schneider) are found in the Malacca Strait. They are represented in South China Sea waters by *H. t. aagaardi* Smith and *H. f. atriceps* Günther (M. A. Smith 1930: 78, 81).

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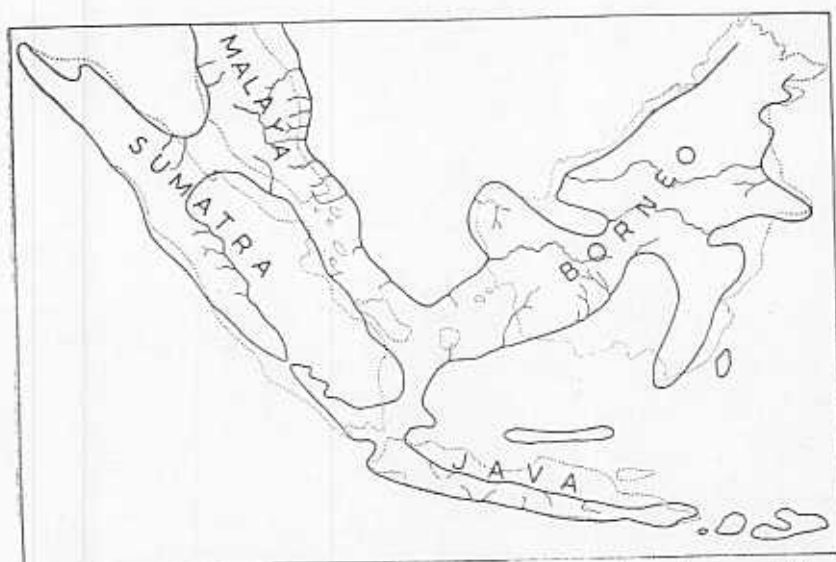


Fig. 1. Palaeogeographic sketch map of the Malaysian Region, showing distribution of land and sea during the Second Interglacial Ingression of the Pleistocene. Redrawn after G. L. Smit Sibinga in L. F. de Beaufort: *Zoogeography of the Land and Inland Waters*. By permission of the author and Publishers.

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4. Auditory and visual signalling

The possession of a stridulating mechanism is widespread among the Grapsoids and is curiously diverse in its development, suggesting

that it has been evolved independently several times. I know of four morphological combinations by which it is arrived at, distributed among genera and species as follows:—

A. A row of closely approximated ridges or tubercles on the inner surface of the chelar propodus is drawn across a single ridge on the ischium of the same cheliped; seen in both sexes of *Ocypode*.

B. A ridge on the inner surface of the merus of the cheliped is drawn along a row, variously constituted, of granules or tubercles, which forms the lower border of the orbit. This is best developed in *Metaplex*, *Helice* and the closely allied *Chasmagnathus*. It is usually confined to the male, but is said by Tesch (1918, p. 119) to be present in both sexes of *Helice tridens* de Haan. It is also found in *Macrophthalmus erato* de Man and *M. quadratus* A.M.-E. and in *Thalassograpsus* [*Brachynotus*] *harpax* (Hilg.).

C. A dentiform process on the inner surface of the carpus of the cheliped is drawn along a suborbital row of granules or tubercles; This is found in *Ilyoplax*.

D. A row of tubercles on the upper border of the chelar dactylus is rasped against a corresponding row on the dactylus of the other chela; found in many species of *Sesarma*.

Type A is so obviously a stridulating mechanism that no discussion of it is necessary. In more than one species it is known to be audible to the human ear. Type B has long been recognised for what it is and the term "musical ridge" has been applied to the ridge on the merus of the cheliped. I have never been able to hear any of these crabs stridulating, but a convincing squeak can be produced by suitably manipulating a preserved specimen of *Metaplex elegans* de Man and I have often seen this species performing the actions which would be expected to accompany stridulation by this means. In *M. elegans* the suborbital ridge bears a large number of small sharp tubercles, so that a true stridulation results. Other species in this category have the suborbital tubercles few and widely spaced so that a series of clicks rather than a musical note is presumably produced. In *Macrophthalmus erato* there are only two such tubercles (but the musical ridge on the merus is unmistakeable) and in *Thalassograpsus harpax* four, the inner one itself finely milled. I do not think the latter species has been recognised as possessing a stridulating apparatus before, but it appears to me indubitable and can be operated by manipulation.

In type C the suborbital tubercles may be calcified and hard, as in *Ilyoplax delsmanni* de Man and its subspecies *serrata* Shen, or chitinous and slightly flexible, a condition found in *I. lingulata* (Rathbun) and *I. punctata* and *obliqua* Tweedie (1935, p. 56 seq.). In all the species they are confined to the male. I have watched *I. delsmanni* jerking its chelae up and down in a way consistent with the interpretation of the type C combination as a stridulating device.

Type D, *Sesarma*, is recorded for the first time. I had long suspected that the dactylar tubercles formed part of a stridulating mechanism, but was never able to form any idea of how this worked until January 1950, when I was watching individuals of *Sesarma eumolpe* de Man in a mangrove swamp near Port Dickson. Two males, feeding round the base of a *Thalassina* mound, encountered each other; after brief sparring one (which had only one claw) retreated, whereupon the other executed a gesture of defiance or triumph which I was fortunately close enough to observe in detail. The crab rose on its feet, twisted one cheliped downwards so that the upper margin of the chela was vertical or even a little overturned, and rubbed the upper margin of the dactylus of the other chela up and down against that of the downturned one, at first rather slowly, but with increasing speed, so that the active chela appeared to be almost vibrating at the end of the performance. I heard nothing but am convinced that the crab was stridulating; the presence of a row of closely and evenly spaced tubercles on each of the chelar dactyli of *S. eumolpe* is consistent with this interpretation. The contortion required to appose the two dactylar margins was so peculiar that it would never be discovered by any deductive method such as manipulating preserved specimens. This type of stridulation is probably also confined to the male sex; the dactylar tubercles are frequently absent in the female and, if developed, never show more than a dim reflection of the male condition.

Purely visual signalling is most conspicuously developed in *Uca*, whose enlarged cheliped is one of the most highly specialised adaptations for this purpose found in the animal kingdom, and the behaviour of crabs of this genus has been closely studied by Pearse (1912) and Crane (1941). The development of a closely similar condition in *Pseudogelasimus* (Tweedie 1937, p. 153), which inhabits mangrove swamp, is of great interest. I have never observed this little crab alive, but there is little doubt that its unwieldy pale-coloured enlarged chela, of which the fingers cannot even close, is analogous with that of *Uca*. Here is a striking case of convergent evolution induced by a similar mode of life, for *Uca* is an Ocypodine and *Pseudogelasimus* a Scopimerine.

The strangely modified enlarged chela of *Potamocypoda* (Tweedie 1938, p. 198), also a Scopimerine, is less easy to interpret. Although apparently an unhandy implement for any kind of manipulation, its curious alignments of granules enclosing masses of felted hair may serve some purpose which only study of the living crab can reveal. The chela is not conspicuously coloured and I would say that it is not used for signalling.

Crabs which practise visual signalling without specialisation of one cheliped include some species of *Macrophthalmus* (e.g. a species with bright blue claws, possibly *M. pacificus* Dana, which I watched at Port Swettenham), and *Heloeius cordiformis*. I have seen this species in Tasmania, jerking its claws up and down outside its burrows, and I noticed the interesting fact that the colour of the chelae varies regionally, being dull greenish-blue in Tasmania and red to purple at Sydney.

In some of the species which I have observed stridulation and visual signalling seem to be combined. The chelae of *Metaplex elegans* and *Ilyoplax delsmanni* are coloured yellow and white respectively, and are conspicuous when the stridulating gesture is being performed. Many *Sesarma* have the chelae bright red or yellow or even distinctively particoloured (*S. versicolor* Tweedie), and most of these have dactylar tubercles whose disposition suggests that they are used in the same way as that observed in the case of *S. eumolpe*.

Whether or not they have realised their biological significance, taxonomists have constantly and profitably used the number, disposition and form of the stridulating tubercles in defining species. De Man seems to have been the first to realise the great importance of exact descriptions of the dactylar tubercles of *Sesarma*. It was failure to recognise this that led Alcock (1900, p. 411 seq.) to lump the species far beyond justification. Ortmann's key (1897-98, p. 359) to *Ocypode* and those of Tesch (1918) to *Metaplex* and *Helice* are based largely on the palmar and suborbital tubercles.

The reason why they are of such great value to the taxonomist is, of course, that they are intrinsically recognitional in character. Differences in their number, spacing and sculpture will impart corresponding differences to the nature of the sound they produce, on exactly the same principle whereby a complicated melody can be accurately and repeatedly rendered by a gramophone record. Similarly the form and coloration of the larger chela of *Uca* affords by far the easiest way of recognising the species; females and males which have lost the larger cheliped are often very difficult to identify.

Recognition of a stridulating mechanism presupposes receptive auditory organs of some kind. The "tympana" on the legs of many Scopimerines are at first sight suggestive of this, but this conception of

them is not maintained by consideration of their incidence. They are found in all the genera except *Potamocypoda*, but are absent in some species of *Ilyoplax*. This is the only Scopimerine genus in which actions and structures suggesting stridulation have been observed, and in some species these are present in the absence of tympana.

A peculiar and consistent feature of the genus *Sesarma* is the presence on the chelar propodus of the male of alignments of small chitinous processes, referred to by taxonomists as pectinated crests or ridges (Kammleisten), their number and disposition being of value as specific characters. They appear to me to be modified setae, usually shortened and thickened. Their form and arrangement in straight, evenly disposed rows has suggested to me the idea that they may be sensory setae modified to intercept and interpret sound waves, and so be correlated with the habit of stridulation. They are present in most species of *Sesarma*, but in *S. johorensis* Tweedie and *S. moeschii* de Man, in which the dactylar tubercles are not developed, and in *S. fasciata* Lanchester, where these tubercles could not possibly function as a stridulating mechanism, the pectinated crests are absent.

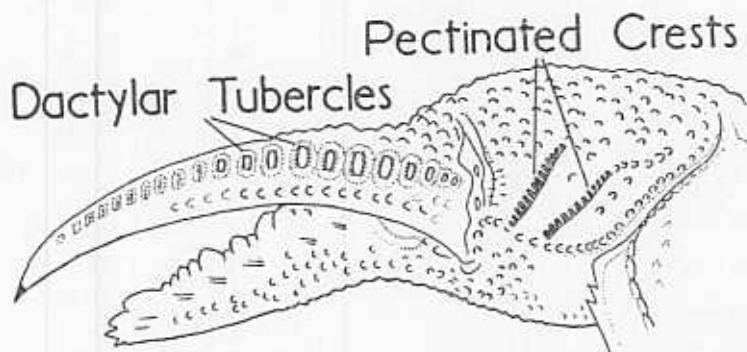


Fig. 2. Right chela of *Sesarma eumolpe*, seen from above. After de Man.

Since the crests are almost always developed only in males this interpretation of them carries the implication that stridulation in *Sesarma* is used for communication, probably to express defiance, between males rather than between the sexes; my observation of the behaviour of *S. eumolpe* is in accordance with this. This may also be so in the case of the other stridulating Grapsoids, but as auditory organs have not been recognised in either sex there is no reason to believe that ability to hear the stridulation is confined to one or the other. Since both sexes of these crabs have very acute vision, at least for the perception of movement, both may be supposed to be able to appreciate visual signalling.

Whichever sex is equipped for reception of the signals, the fact that the structures specialised to produce them are, in all but one genus, virtually confined to the males is evidence for supposing that their main implication is sexual, their purpose either to attract and stimulate the female or to assert dominance over other males.

In the case of aquatic crustaceans it seems most likely that traffic between the sexes is promoted mainly by perception by an olfactory sense of chemical substances released into the water. Observation of the amphibious Grapsoids has persuaded me that all their vital activities like feeding and mating are conducted during the low tide period in an atmospheric environment. Both the productive and receptive organs needed to deal with chemical stimuli are very different in aquatic and terrestrial animals, and in their evolutionary passage from a purely aquatic existence those of the Grapsoids may be supposed to have failed them. Their place was taken, not by an analogous atmospheric system, but by auditory and visual communication.

The morphological diversity of these devices and the extremes to which they appear to have been carried are, perhaps, explained by consideration of the mode of life of these crabs. Nearly all of them are deposit feeders subsisting on the surface film of stranded plankton or other organic matter on the sand or mud, which is renewed at every tide, and which is almost as liberally available as is oxygen for respiration. By burrowing in the mud or sand each crab is able to make a refuge to which it can readily flee from the attack of a terrestrial predator, and from which it need not venture far in search of food. In observing a colony of *Uca* the slightest incautious movement results in their instant disappearance, each into its own burrow. A few birds, such as Kingfishers, may prey on these crabs, but I believe that they are not seriously harassed by predators. Presumably they shelter in their burrows when the tide covers their feeding grounds (*Dotilla* and *Scopimera* are known to do so) and so are largely protected from aquatic enemies.

The average Grapsoid, then, has no difficulty in finding its food and little in avoiding its enemies, but both these advantages are associated with a stay-at-home sort of existence. Under these conditions selection pressure will act not so much in favour of those which can feed themselves and avoid destruction, but of those which can find a mate and reproduce their kind, and a variety of adaptations to promote sexual success will be evolved, even though they render the individual conspicuous, as any signalling device must do, or even hamper its movements and halve its food-gathering capacity as well, as does the modified chela of *Uca* and *Pseudogelasimus*.

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5. *Metopograpsus gracilipes* de Man.

In a revision of the genus *Metopograpsus* (1949) I reported that *Metopograpsus intermedius* Milne-Edwards (1853) is represented in the Musée d'Histoire Naturelle in Paris by two cotypes belonging to distinct species. One, the smaller, is a specimen of *M. thukuhar* (Owen 1839), the other is identical with the form referred to *M. messor* var *gracilipes* by de Man (1891: 49), which I showed to be a distinct species. I recorded this species under the name *M. gracilipes* de Man, stating that "the name *intermedius* is composite and cannot be used".

Later doubts about the correctness of this taxonomic procedure led me to consult Dr. Isabella Gordon of the British Museum, and she asked Dr. L. B. Holthuis of Leiden for his opinion. Both these authorities are agreed that it would have been better to designate the larger of Milne-Edwards' cotypes as lectotype and so to establish *intermedius* as the valid name for the species, with *gracilipes* of de Man standing as a synonym.

This could still be done, but a change in nomenclature after the publication of a generic revision is bound to lead to confusion. The two authorities whom I consulted have suggested that *gracilipes* would be established as a valid name if the smaller of Milne-Edwards' cotypes were designated lectotype of his species *intermedius*.

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In my capacity of the author of the most recent revision of the genus, I therefore designate the smaller of the two cotypes of *Metopograpsus intermedius* Milne-Edwards as lectotype of the species. The effect of this is to make the name *intermedius* a junior synonym of *M. thukuhar* (Owen), and to establish *gracilipes* de Man as the valid name for the species represented by the larger cotype of *intermedius* and described under the name *gracilipes* on page 470 of my revision of 1949.

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